Dynamics of some forests in Kwa Zulu-Natal, South Africa, based on ordinations and size-class distributions

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Received 21 February 1995; revised 14 July 1995

Indigenous forest in Kwa Zulu-Natal has been fairly well described; however, very little has been published on its dynamics. There is, to our knowledge, nothing published on disturbance regimes, dendrology and life histories of constituent species. In order to assess the conservation status, management and sustainability of these forests we have developed a dynamic framework by synthesizing information collected in many randomly located 400-m^2 sample plots in a range of forest types. We reasoned that ordinations between understorey and overstorey data from these plots would indicate the grain of a forest. Fine-grained forests would be indicated by close proximity, in ordination space, of understorey and overstorey. Similarly we argue that a predominance of canopy species with negative exponential size-class distributions should typify the more fine-grained forests. Our analyses suggest the following dynamics spectrum: from fine-grained upland forests with *in situ* recruitment from advanced regeneration for most canopy species, to coarse-grained lowland forests where canopy species have flat size-class distributions and spatially variable recruitment. These results are discussed with a view to the conservation of the different types.

Die inheemse woude in Kwa Zulu-Natal is al redelik goed beskryf. Daar is egter tot op hede baie min inligting oor die dinamiek van die woude gepubliseer. Sover ons kennis strek, is daar geen artikels oor versteuringspatrone, dendrologie en die lewensgeskiedenis van die individuele spesies gepubliseer nie. Ons het 'n dinamiese raamwerk ontwikkel deur die inligting wat op verskillende ewekansige geplaasde persele van 400 m^2 in verskeie woudtipes versamel is, saam te stel en te interpreteer. Die bewaringstatus, bestuur en volhoubaarheid van hierdie woude kan met behulp van die raamwerk ondersoek word. Ons voer aan dat die klassifikasies van die onder- en kroonbos van hierdie persele die grein van 'n woud sal bepaal. Fyngrein-woude word deur die mate van naburigheid tussen die kroon- en onderbos in die klassifikasieruimte aangedui. Ooreenkomstig voer ons aan dat fyngrein-woude 'n meerderheidsteenwoordigheid van kroonspesies met 'n omgekeerde-J-grootteverspreiding sal hê. Ons analise stel die volgende dinamiese spektrum voor: van fyn-grein hoogliggende woude met *in situ*-hervestiging van gevorderde regenerasie vir die meeste kroonspesies, tot die grof-grein laagliggende woude met kroonspesies met plat grootteverspreidings en verandelik-gespasieerde regenerasie. Hierdie resultate word bespreek in terme van die bewaring van verskillende woudtipes.

Keywords: Competitive hierarchy, disturbance, forest, grain, management, patch dynamics.

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Introduction

Conservation biology is currently undergoing a shift in focus from the species level to the level of landscape ecology where processes are emphasized (Pickett et al. 1992). Coupled with this shift, the political, economic and social climate in South and southern Africa is changing rapidly with factors such as land allocation, sustained utilization of natural resources and a critical review of conservation receiving attention. At present most indigenous forest patches in South Africa are strictly protected and managed as conservation areas. Rural populations derive very little benefit from this situation, which has lead to the questioning of the value of forest patches. The forests have traditionally been a source of a variety of resources such as poles, sticks, laths, medicines and food. In order to ensure their value, and therefore their conservation, it has been suggested that sustainable utilization of these resources is necessary. A sound understanding of the dynamics of the forest communities is required if the utilization of forest resources is to be sustainable. In the province of Kwa Zulu-Natal on the eastern seaboard of South Africa, indigenous forests are scattered throughout the region and cover an area of approximately 100 000 hectares. This represents only about 1.05% of the total surface area (Cooper 1985). To date, most of the literature on these forests is descriptive. Apart from a few sources (Cawe 1986; Moll 1968, 1972a, 1972b) which make some suggestions about forest development and the effects of human-induced disturbances, and suggest reasons for the apparent lack of regeneration of canopy species, very little of the literature addresses possible mechanisms involved in the dynamics of the forest communities. For instance, there is very little information on disturbance regimes in the forests and life histories of constituent species.

This lack of information on forest processes in Kwa Zulu-Natal makes it very difficult to know what level of utilization is sustainable. This prompted us to develop a framework of forest dynamics which could act as a starting point for understanding what levels of utilization might be sustainable. Our aim was to synthesise data collected for descriptive studies into a dynamics framework.

Theoretical background

Given that all plants have shared requirements for a few essential resources (Grubb 1977; Harper 1977), we may logically expect that there will be inclusive fundamental niches along natural environmental gradients. In such circumstances, competitive hierarchies can determine species-realized niches, and therefore distri-butions along environmental gradients (e.g. Keddy 1989). In forest ecosystems, shade tolerance is the primary criterion used for arranging tree species into a competitive hierarchy (Horn 1971, 1981; Keddy & MacLellan 1990), with the most shade-tolerant species situated at the top of the hierarchy. Forests can be seen as spatial mosaics of structural phases which change over time as a result of dynamic processes, where the winning competitors for mainly the light resource, determine the canopy composition. Dynamic processes are usually associated with disturbance, which in forests often results in gap formation. This is therefore regarded as the most important disturbance factor in forests and many (e.g. Denslow 1985; Pickett & White 1985; Whitmore 1989) consider gaps to drive the forest cycle. This perception is not without its critics (e.g. Terborgh 1988; Lieberman *et al.* 1989; Dirzo & Miranda 1990) and the importance of gaps has and is receiving a great deal of re-evaluation (see review in *Ecology* 70, 1989).

In spite of the reservations expressed by some, we felt that gap dynamics and the varying tolerance that tree species have for shade is the best starting point for the development of the dynamics framework. An issue which needs clarification when dealing with patch dynamics within forest communities is scale. The term 'patch' typically implies a discrete and internally homogeneous entity, yet such patches are seldom observed in nature (Kotliar & Wiens 1990). Instead, hierarchical mosaics of patches within patches occur over a broad range of scales (Wiens 1976; Senft *et al.* 1987). In their book on patch dynamics, Pickett & White (1985) avoided defining a patch altogether, although they indicated several important components of patch structure: 'patch implies a relatively discrete spacial pattern, but does not establish any constraints on patch size, internal homogeneity or discreteness'. This difficulty in defining patches according to a scale is closely related to the whole controversy of classification and defining communities (see for example Kent & Ballard 1988). In order to overcome this problem of scale we use the concept of grain (e.g. Midgley *et al.* 1990) in which they incorporate the rela-tive scale (frequency, area) of disturbance type with the life-history attributes of the species present, to classify forest communities as being either coarse- or fine-grained. The grain of a forest therefore reflects the scale of dynamic processes.

There are a number of ways in which the grain of a forest community can be established from the available plot data. Firstly, one can simply compare the composition of the canopy with that of the sub-canopy and shrub layer. These data can then be used to develop a Markovian replacement model (*sensu* Horn 1981), where one measures which species are growing beneath which, and a prediction of which species are most likely to replace which, is made. In a fine-grained forest, one would expect to find that most of the species occupying the canopy are also present in the sub-canopy. These species would be replaced from advanced regeneration and all would be relatively shade tolerant. The scale of variation from patch to patch in this type of forest would be small and therefore it would exhibit a fine grain. Midgley *et al.* (1990) used this approach to show that Afromontane forests of southern Cape plateaux in South Africa are fine grained.

A second approach is to analyse the size-class structure of the important tree species in each community. In a fine-grained forest one would expect to find that most trees have an inverse-J-shaped, curved size-class distribution. In other words there should be many small trees and few large trees (Figure 1). In more coarse-grained forests the size-class distributions of various species would differ according to their position on the hierarchy of competition for light (degree of shade tolerance). Light-demanding species, which will only survive in gaps, would exhibit unimodal or bimodal bell-shaped curves (Figure 1). It is therefore important that the size-class distributions within plots are assessed to see if large and small trees of the same species co-occur.

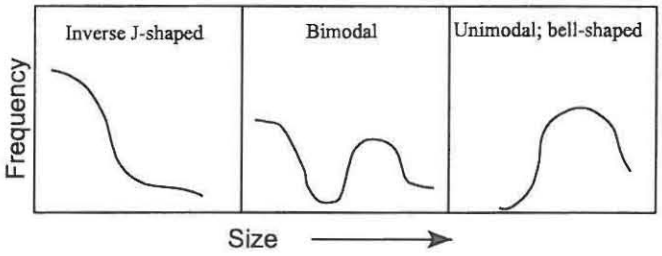

Figure 1 Three possible curve shapes for size-class distributions of tree species within forests.

Study area

The indigenous forests of Kwa Zulu-Natal, South Africa have been broadly classified into two types, the Afromontane forests (White 1978) of the uplands, and lowland subtropical forests of the Indian Ocean coastal belt (Moll & White 1978). These two main forest types have been subdivided into a further eight subtypes (Edwards 1967; Moll 1978; White 1978; Cooper 1985). These are the montane *Podocarpus* forests and the mist-belt mixed *Podocarpus* forests which are Afromontane, and the coastal scarp forest, coastal lowlands forest, sand forest, swamp forest, riverine forest and dune forest which are lowland subtropical types.

This synthesis relied heavily on available data and therefore a sample from all forest types was not possible. Table 1 provides details of data that were used.

Methods

Sampling methods

All the plot data were recorded from standard 0.04-ha circular plots (radius 11.28 m) which were randomly located in mature homogeneous stands of forest. As far as possible, similar communities were sampled within each forest type. The heights of all woody species above knee height (0.5 m) were estimated and recorded. The diameter at breast height (DBH) of all woody species with a DBH > 5 cm was also measured and recorded. In each plot, note was also taken of

Table 1 Forest types, number of samples per forest and the source of data used for analysis

Forest type	No. of plots	Source of data
Montane *Podocarpus* forests	10	Everard (1992)
Mistbelt mixed *Podocarpus* forest	22	Everard (1992)
Coastal scarp forest	10	Everard (1992)
Coastal lowlands forest	19	Gordon (unpublished)
Dune forest (south coast)	56	MacDevette & Gordon (1989)
Sand forest	7	Everard (1992)

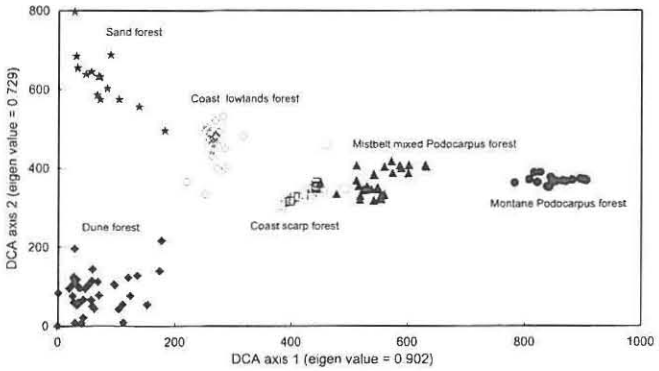

Figure 2 An ordination diagram, produced by DECORANA, for all the plot data.

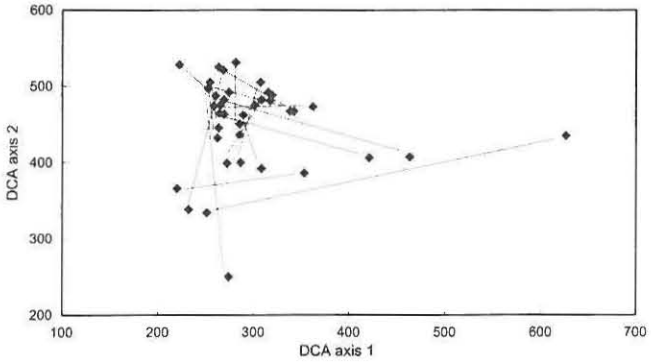

Figure 3 A subset of the ordination diagram showing the coastal lowlands forest plots. The lines link the sub-canopy with the canopy from the same plot that was sampled in the field. The length of the lines linking the two layers indicates the degree of similarity between the two layers.

the general appearance of the forest, with estimates of canopy, shrub and ground-layer height, and the percentage cover of these layers being made and recorded.

Data analysis

For the purpose of assessing which species are most likely to replace which, and the development of a Markovian type model, plot data were separated into two sub-plots, one sub-plot containing canopy data and the other sub-canopy/understorey data. This data set containing the sub-plots was then ordinated using DECORANA which is a programme for conducting detrended correspondence analysis (Hill 1979). Frequency data (stems per plot) were used in the ordination. A comparison of the ordination distance between the two sub-plots shows how the canopy differs from the sub-canopy/understorey. In a fined-grained forest these distances would be close, indicating that the canopy contains a similar combination of species to the sub-canopy/shrub layer. For this analysis woody shrub species that never reach the canopy (understorey species) were omitted, as they would show the sub-canopy to have a different composition from the canopy and the resulting variation between the ordinations would be misleading. We used the mean distance between the plotted point of the canopy, and sub-canopy/shrub from the same plot, giving an indication of the similarity, and therefore grain. When the mean distance between the two forest layers from the same sample is small, then the forest has a similar sub-canopy/shrub species composition to the canopy, which indicates a fine-grained forest. To make the sets of ordination distances comparable, it was necessary to ensure that the total variation for each data set was constant. This was achieved by grouping data from various forests to produce an ordination, and then comparing the distances between the canopy and sub-canopy/shrub positions of sub-sections of the ordination diagram. The mean distance between canopy and sub-canopy/shrub plots were calculated using axes 1 and 2 from the sample scores produced by DECORANA.

The size-class structures of the dominant tree species of the various forests were analysed by plotting the numbers of individuals per size class and interpreting the general shape of the graphs visually. A species with many more small than large individuals, therefore, conforms to the inverse-J size-class distribution. This species can be assumed to be shade-tolerant as it is able to regenerate under the prevailing canopy. An abundance of shade-tolerant species in a forest community would indicate a fine-grained forest. A species with few or no small individuals and many large individuals would indicate that the species regenerates poorly or not at all under the prevailing canopy. It could be argued that these species are shade intolerant, and a predominance of these species in a forest community would indicate a coarse-grained forest.

Results

Comparison between the canopy and sub-canopy layers

Figure 2 presents an ordination diagram for the entire data set. Axis 1, which reflects the greatest variation in the data set, apparently correlates strongly with altitude. It separates forest types according to the existing classifications. Subsets of this ordination diagram have been used to make comparisons between the canopies and sub-canopies of the different forest types.

Figure 3 presents a subset of the ordination diagram (Figure 2) for coastal lowlands forest. The lines in the ordination diagram link the canopy and sub-canopy of the same plot. The length of these lines in ordination units gives an indication of the degree of similarity in species composition between the canopy and sub-canopy. Table 2 presents the mean lengths of these lines for all the forest types. The greatest difference between the canopy composition and the sub-canopy/shrub layer composition, after non-canopy species have been removed from the data set, was found in coastal lowlands forest. In general the lowlands forests show greater variation between the canopy and sub-canopy layers than do the uplands forests.

Size-class distribution

The frequency per size (DBH) of the six most common tree spe-

Table 2 Mean distances for each forest (ordination units) between sub-plots of the sub-canopy/shrub composition and canopy composition from the same sample plots. The distance apart refers to how far apart (in ordination units) the canopy plots are from the sub-canopy plots on the graph and gives an indication of how similar the sub-canopy composition is to the canopy composition

Forest type	Axis 1	Axis 2	Distance apart
Montane *Podocarpus* forest	59.44	10.44	60.35
Mistbelt mixed *Podocarpus* forest	40.57	19	44.80
Coastal scarp forest	37.1	35.6	51.42
Coastal lowlands forest	77.57	64.52	100.90
Dune forest	32.4	42.9	53.76
Sand forest	37.71	65.28	75.39

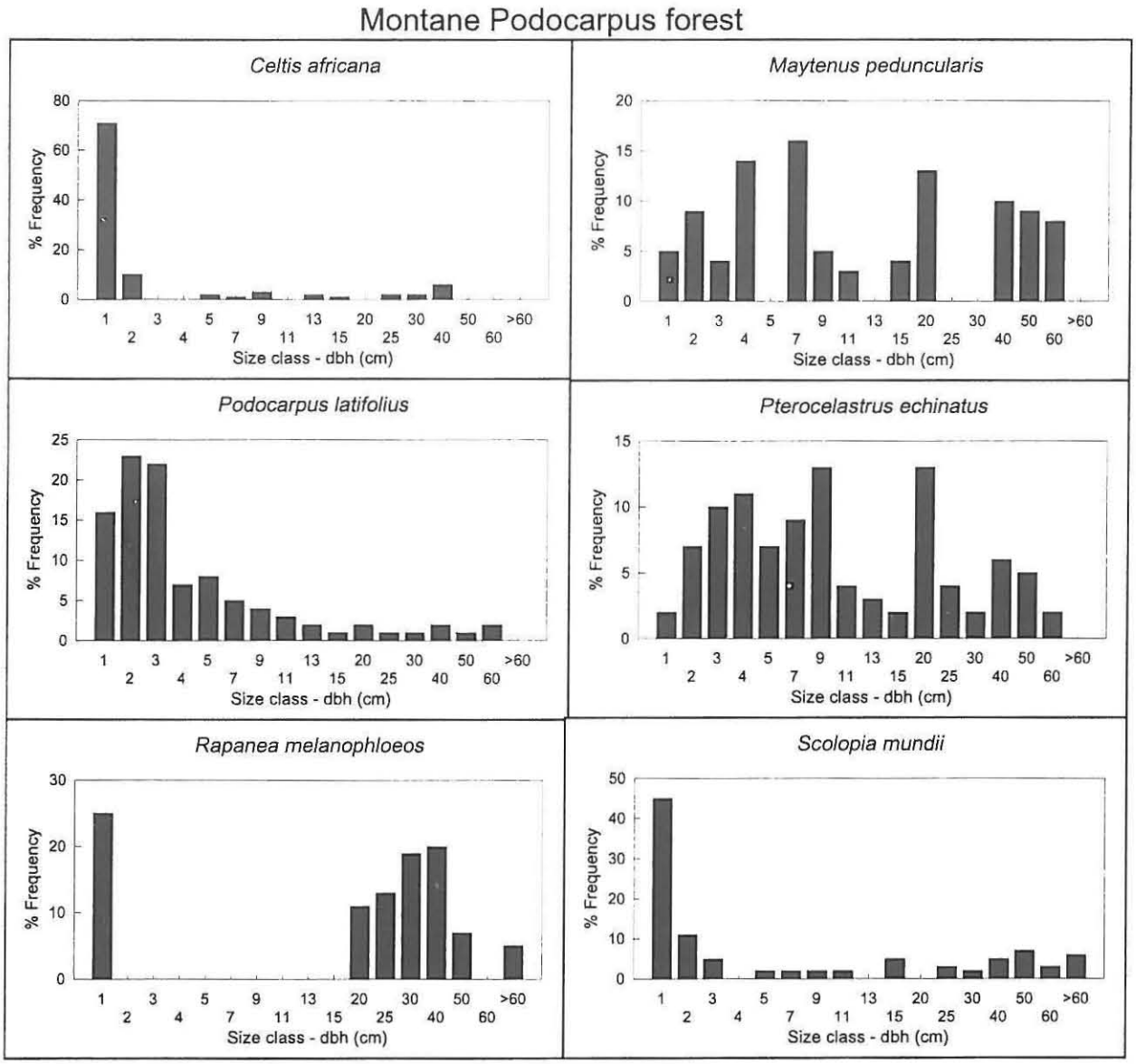

Figure 4 The size-class distribution for the six most common canopy trees in montane *Podocarpus* forest.

cies in the canopy of the various forests are graphed and presented in Figures 4 to 9. It was only possible to use six species per forest community because most of the communities had only six common species as part of the canopy. Species other than the six or seven most dominant species occurred infrequently, which made it impractical to sample enough plots to ensure sufficient indivi-duals were recorded to construct size-class distribution curves for these rarer species. Figure 4 presents the results for the high-altitude Afromontane forests, which suggest that this forest is mixed in its composition of shade-tolerant and shade-intolerant species. Some species consist of many small and few large individuals (shade tolerant) while others consist of as many or more large individuals than small individuals. The mistbelt mixed *Podocarpus* forests are dominated in the canopy by species that show the more typical pattern with many more small than large individuals. The coastal scarp forest has only two of the six most dominant species that show the typical inverse-J-shaped curve, the other four species display different patterns, with a large proportion of the individuals being large. The graphs for the coastal lowlands forest (Figure 7) show that of the six most common tree species in this forest, two have a normal size-class distribution. All the other species produce flat or unimodal curves. The dune forests are also mixed in nature with some species indicating normal size-class distributions and others deviating from this pattern. The sand forests in general show that the dominant species are made up of many small individuals but few middle-sized trees, usually with an increase in large individuals.

Grain

The ordination comparing the canopy with the sub-canopy needs to be interpreted in conjunction with the size-class distributions of the common tree species, to identify the grain of the forests. Forest communities with sub-canopies that are very similar in composition to the canopy and have canopy species that have more small than large individuals indicate that recruitment to the canopy is occurring from advanced regeneration. Turnover of individuals is therefore occurring on a small scale and the forest can be interpreted as being fine-grained. When the sub-canopy and canopy differ, it suggests that some unique disturbance or event (e.g. cyclone or fire) is required for recruitment of canopy trees. The dynamics of such a forest may therefore occur at a

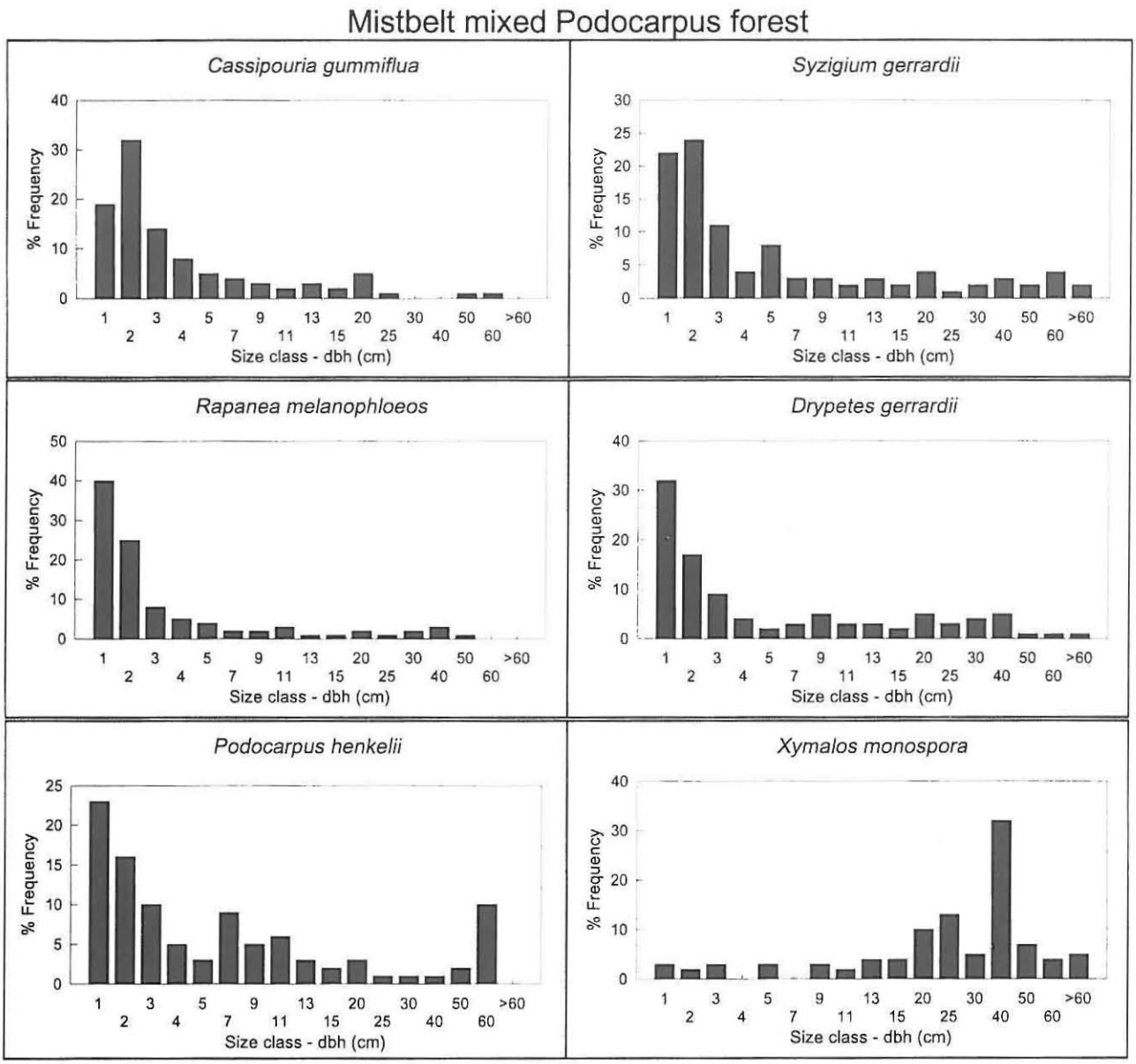

Figure 5 The size-class distribution for the six most common canopy trees in mistbelt mixed *Podocarpus* forest.

much larger spatial scale and these can be classified as coarse-grained forests.

Our results indicate that the forests can be classified as having different grains. The finest-grained forest, according to these results, appears to be the mistbelt mixed *Podocarpus* forest, with the dune forests, coastal scarp forests and the Afromontane *Podocarpus* forests fitting onto a gradient of forest grain in order from relatively fine grained to relatively coarse grained. The coastal lowlands forests are classified as being very coarse grained.

Discussion

The floristic composition of the indigenous forests in Kwa Zulu-Natal is reasonably well known and has been subjected to many analyses (see Everard 1991 for a review). It is quite clear that the forests show considerable floristic variation and are easily classified into forest types. Even the ordination of the available data used for this study (Figure 2) indicates that the forests show considerable variation in species composition. The results of this study certainly indicate that not only do the forests vary in floristic composition but also, they show considerable variation in grain.

With the use of the ordination technique we are able to show that in mistbelt mixed *Podocarpus* forest the canopy composition is very similar to that of the sub-canopy. The size-class distribution for the dominant canopy trees in this forest confirms that the sampled plots all had many small individuals co-occurring with the large individuals of the same species.

In the event of a gap causing disturbance, a number of things can occur. A fast-growing, shade-intolerant species could quickly colonize the gap and grow up to become part of the canopy, the existing shade-tolerant species could dominate and close the gap, or the gap could be closed laterally. In mistbelt mixed *Podocarpus* forest, evidence for the former process to be common was lacking – none of the common canopy species appeared to be shade intolerant.

The ordination results for the dune forests showed that there was greater variation between the canopy and sub-canopy than was found in mistbelt mixed *Podocarpus* forest. The size-class distributions of the dominant canopy species for these forests also indicated that most species are shade tolerant, with large and

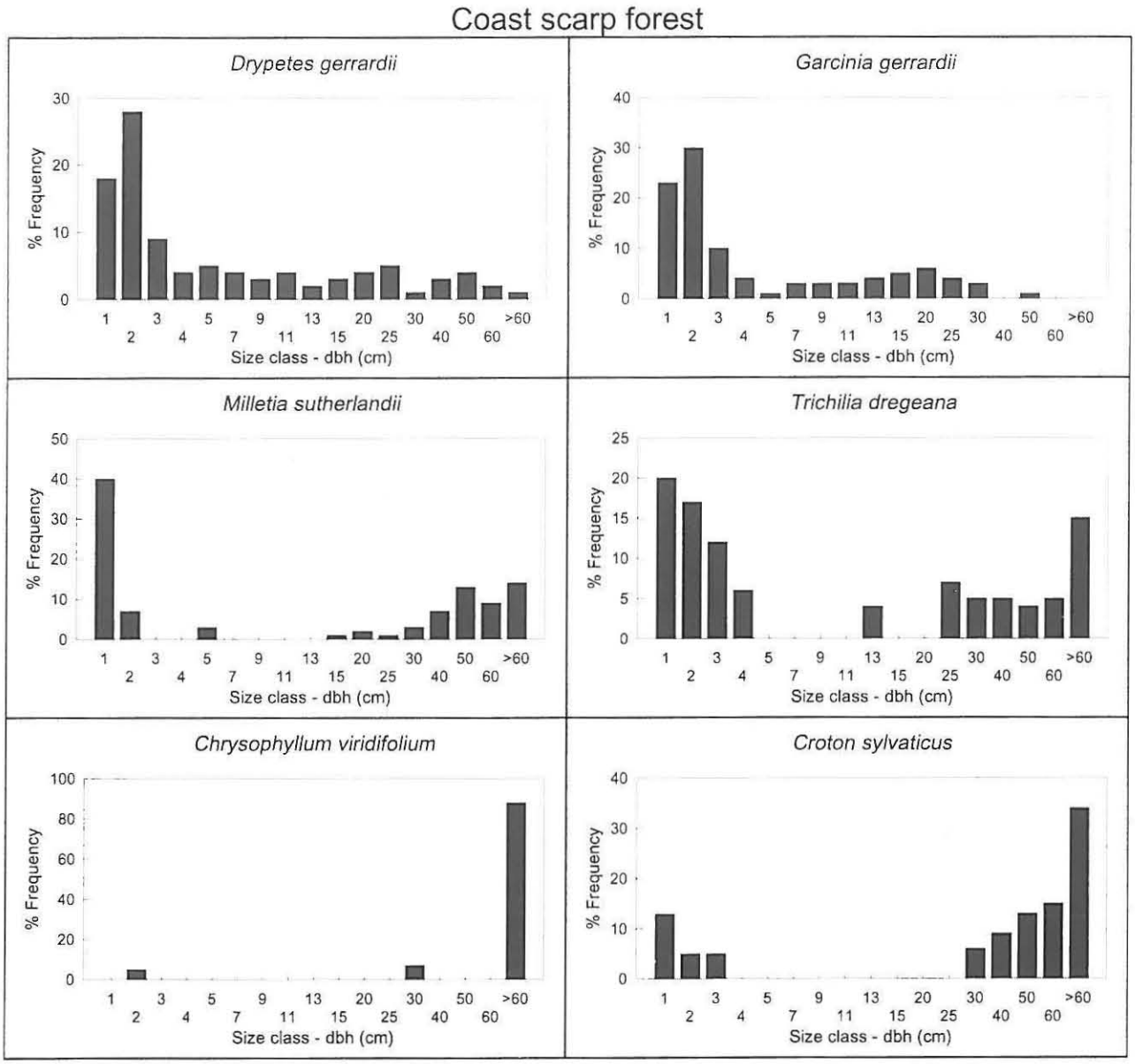

Figure 6 The size-class distribution for the six most common canopy trees in coast scarp forest.

small individuals co-occurring. Some species though, produced distribution patterns indicating that small individuals are uncommon in the forest, which could indicate that they are shade intolerant and require a disturbance to become established and form a component of the canopy. The dune forests have been relatively undisturbed by humans since colonial settlement (MacDevette & Gordon 1989), which means that the forest communities should have reached a level of dynamic stability. The results of the size-class distribution of the dominant sand forest species also indicates that this forest's canopy consists mostly of species that appear to be shade tolerant.

Coast scarp forest is shown to have differences between the composition of the canopy and the sub-canopy, although, in general, these differences are small. The analysis of size-class distributions indicates a mixed forest, suggesting some species are not regenerating under the canopy. The canopy comprises both shade-tolerant and shade-intolerant species. The mixed canopy can be explained by the fact that these forests are situated on an uplifted complex of granite and schist (Huntley 1965) which has resulted in generally shallow soils. This, together with the fact that the forests are situated on the coastal scarp means that the canopy is frequently exposed to strong winds which regularly blow adult trees down. Gap-forming disturbances are therefore a common feature of these forests, which allow a large proportion of the canopy to consist of shade-intolerant species. Observations of gaps during the survey of these forests revealed that gaps were indeed quickly occupied by species such as *Trichilia dregeana, Croton sylvaticus* and *Chrysophyllum viridifolium*. The gaps are generally small and scattered, resulting in a forest with an intermediate grain. The upland forests in the Drakensberg in western Kwa Zulu-Natal show similar patterns and prevail under similar conditions, with disturbance localized to tree-falls. These forests are also intermediate in grain.

An example of an extremely coarse-grained forest type is coast lowlands forest which appears to consist of communities that are successional in nature. In the early successional communities all the common species are shade intolerant but in the mature core forests there is a greater component of shade-intolerant species. The interpretation here is that this forest has developed under large-scale disturbances. In the absence of disturbance the forest would probably become more fine grained but many species would be lost (van Wyk & Everard 1993).

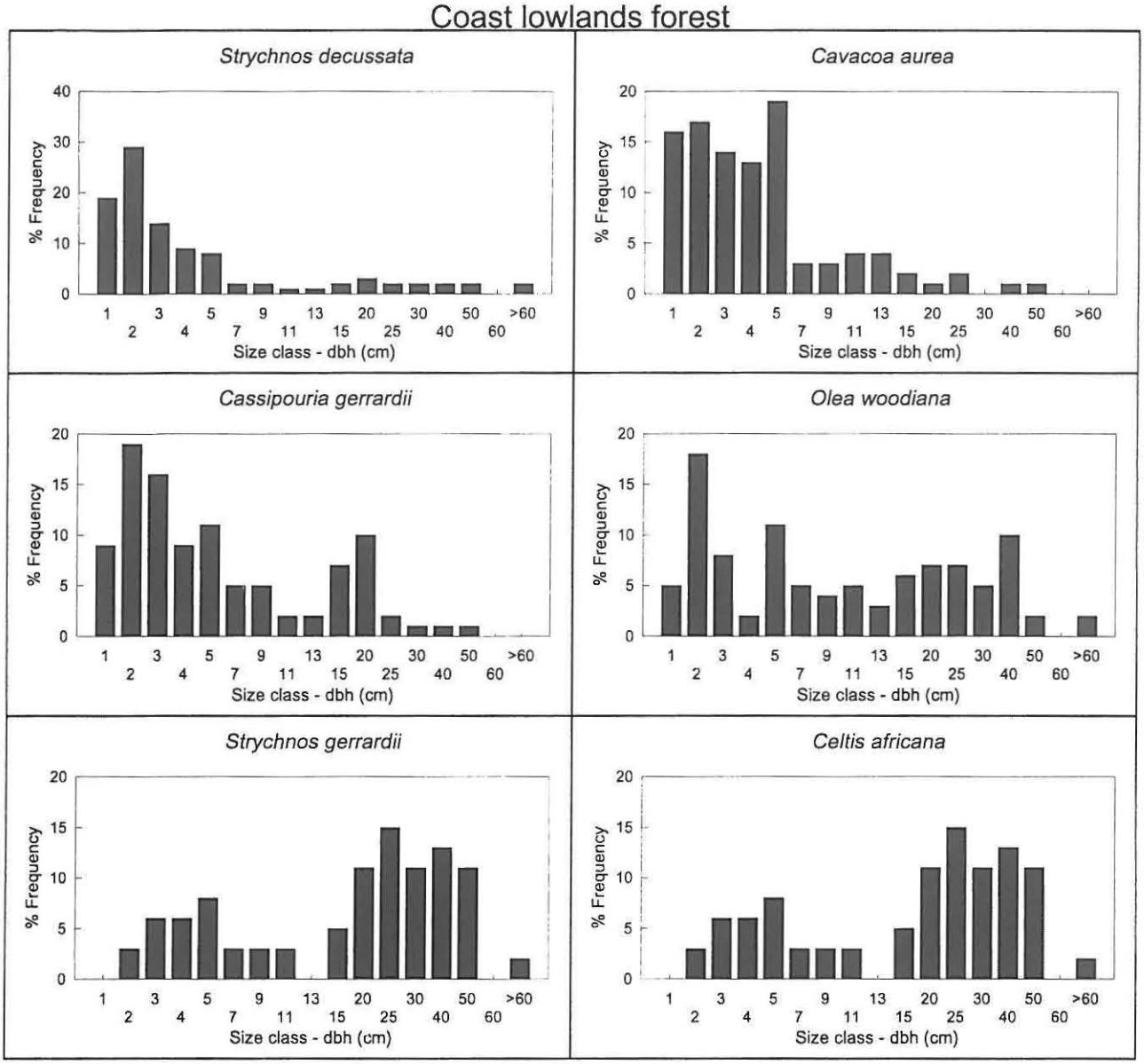

Figure 7 The size-class distribution for the six most common canopy trees in coast lowlands forest.

Relevance of grain to the management of forest communities

The grain of a forest relates to the scale on which the 'normal' dynamic regeneration processes occur. If these processes occur on a small scale then it is logical to assume that small patches of forest can exist as an entity and be sustainable. In a coarse-grained forest, dynamic processes occur over a large scale and therefore large patches of forest must be protected if the forest is to remain a sustainable functional unit. An assessment of grain, therefore, allows one to assess to a certain extent what the minimum sustainable patch size of a forest is, with regard to tree regeneration and patch dynamics. Grain at this level does not take other processes, such as pollination and seed dispersal, into account. These pro-cesses could quite easily function on a much larger scale than the dynamics of the trees, which could have a bearing on the sustainability of a small patch of forest, even if it is a fine-grained forest.

The classification of forest function in the form of identifying the grain of the forest also allows one to assess the effects of certain treatments to which the forest might be subjected. For example, when managing a forest it is necessary to know what level of disturbance should or should not be allowed within that forest. In a relatively coarse-grained forest, regular disturbance is required, in order to maintain the full complement of species. If the disturbance is removed (e.g. fire protection) then one would expect shade-tolerant species to increase, to the detriment of the shade-intolerant species. The total removal of disturbance from this type of forest could thus ultimately lead to the loss of certain species. Good examples of this type of forest are the coast scarp forests where the elimination of frequent gap-forming disturbances would lead to the canopy composition ultimately changing, to the detriment of species like *Trichilia dregeana, Croton sylvaticus, Milletia sutherlandii* and *Chrysophyllum viridifolium,* which are at present important components of the canopy.

In a very coarse-grained forest, such as coast lowlands forest, it might be necessary to allow an occasional large-scale disturbance to occur, where a number of trees are removed to create a large gap. If this proves to be the case, then disturbance such as migratory slash and burn, as was practised by the inhabitants of the region in precolonial times, may have minimal effects.

A knowledge of the grain of a forest also allows the manager to make better judgements on the exploitation of resources in the

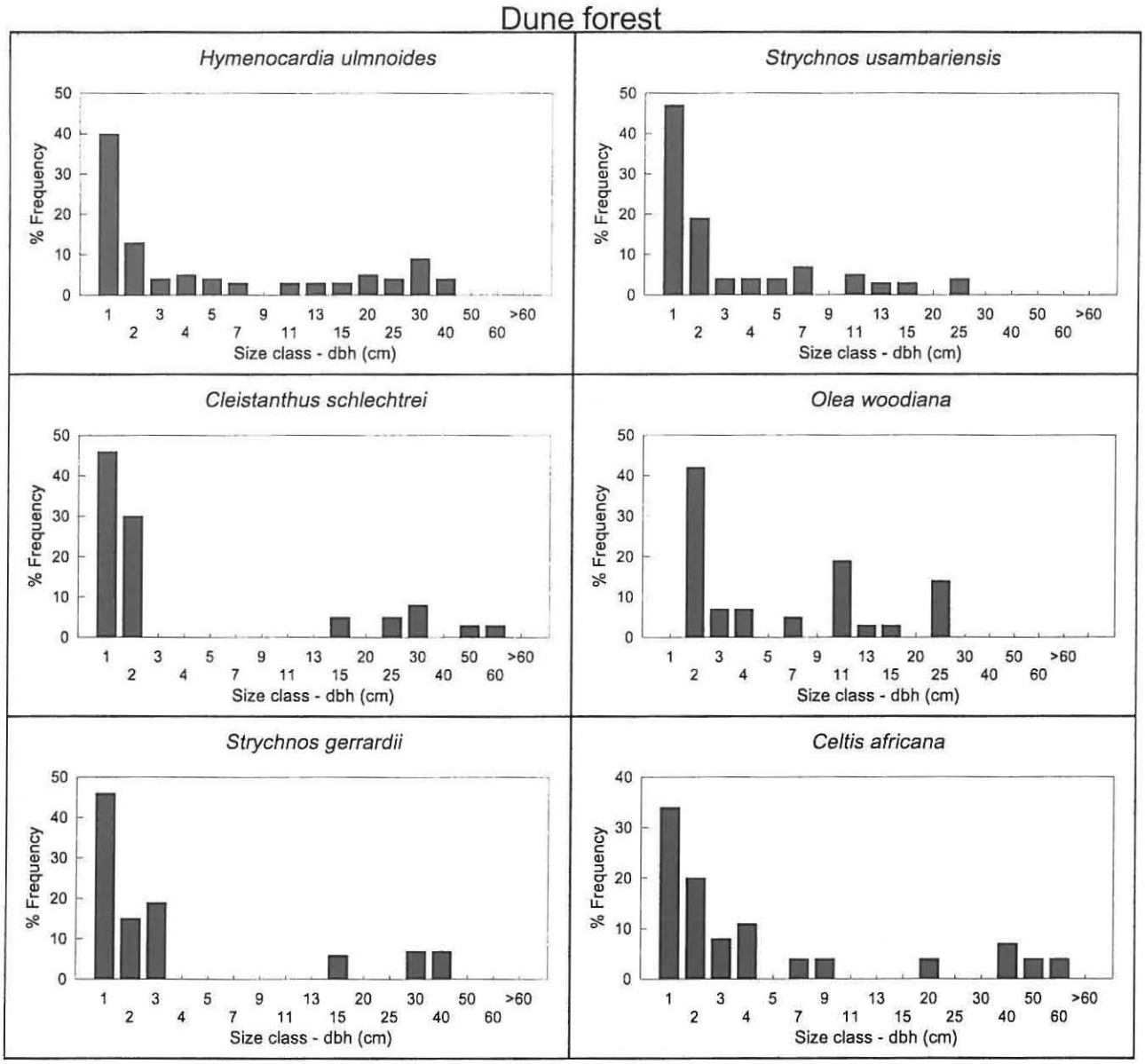

Figure 8 The size-class distribution of the six most common canopy species in the dune forest.

forest. One of the most important products required from forests by rural populations is poles for building material. Fine-grained forests generally have huge supplies of poles from most species and the exploitation of this resource, if sustainable, would probably have very little effect on the long-term composition of the forest. In coarser-grained forests, however, the supply of poles might be confined to the shade-tolerant species which are growing in the understorey in abundance. If, however, poles of a shade-intolerant species in gaps were to be exploited, this species could be lost to the forest, as it is restricted to gaps, and therefore generally not abundant.

Conclusions

The approaches of comparing the canopy and sub-canopy by ordination, and describing the size-class distributions of important canopy species has proved to be workable and provides a clear indication that the grain varies between forest types. As grain in this context relates to the scale at which dynamic processes of canopy trees occur, this study has suggested that it is feasible to develop a dynamics framework for indigenous forests.

Results identify mistbelt mixed *Podocarpus* forest to be relatively fine grained, dune forest and sand forest to be mixed with an intermediate grain. Coast scarp forests were found to be coarse grained and coast lowlands forest very coarse grained. The analysis has only been conducted on a small portion of the forests in Kwa Zulu-Natal and was aimed at the level of forest type.

The real value of developing a functional classification for forest communities lies in the possibility of hypothesizing about the dominant processes within a forest. Appropriate management policies for forests can then be developed. The lack of time and funds makes it impossible for every forest to be studied in detail, so a method of functionally classifying them is important. Investigations into relating the grain of forests to environmental factors such as climate, altitude, geology, soils and possibly prevailing disturbance processes need to be conducted. If this proves to be possible, then a simple rule-based model or expert system could be produced to help forest owners and managers develop sound management policies for their forests, which must include sustainable utilization if the forests are to have any value to rural populations.

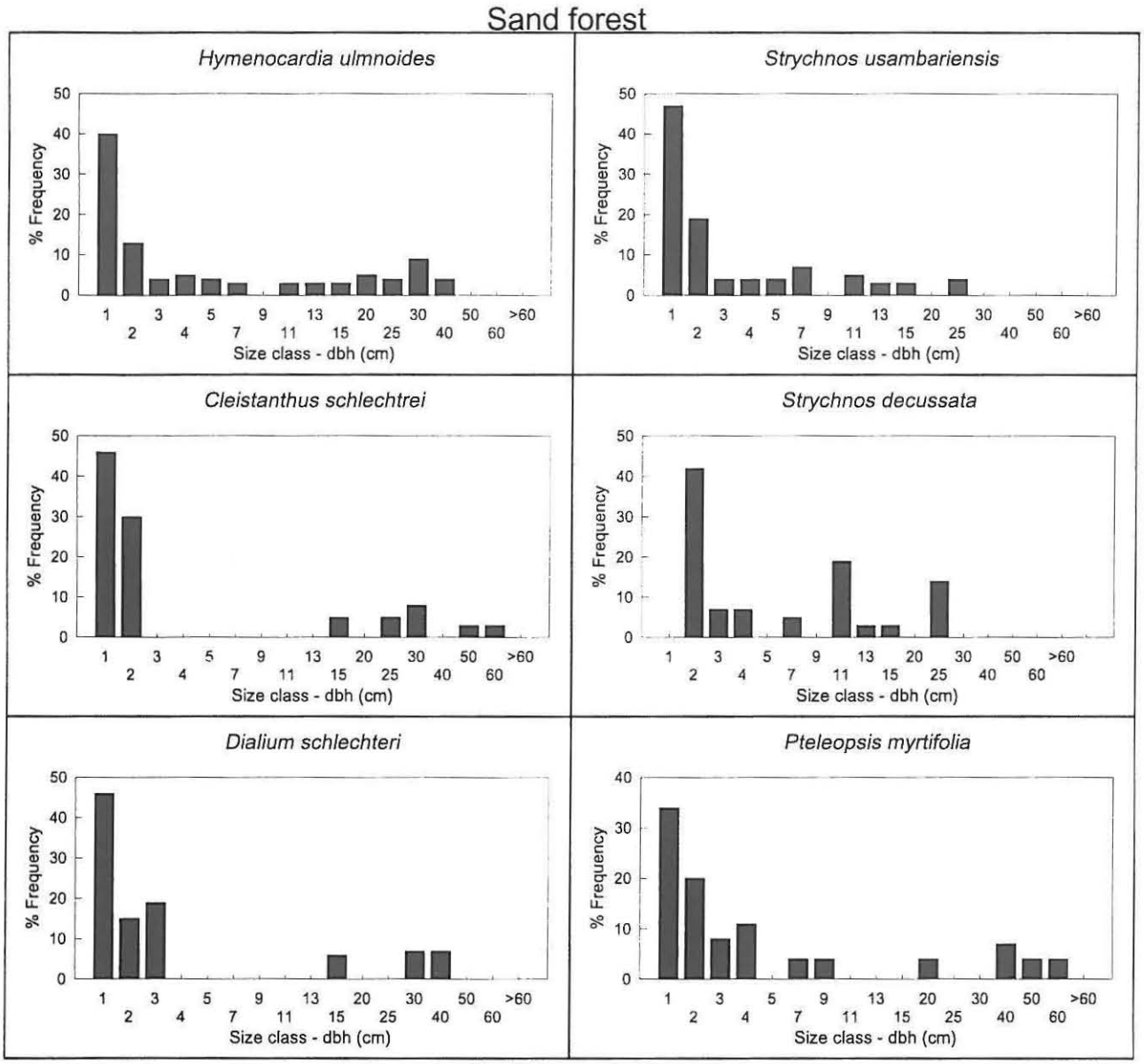

Figure 9 The size-class distrubution of six common tree species in the canopy of sand forest.

Acknowledgments

This research was jointly funded by the Department of Environment Affairs and the Department of Water Affairs and Forestry, Forestry Branch. Many of the data were provided by Ian Gordon who conducted much of the fieldwork. Graham von Maltitz contributed to the development of the ideas presented in this report through lively discussion with the authors.

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